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Managing time in a changing world

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Chapter 4

Temperature at the wintering grounds affects arrival date and predicts the fitness landscape at the breeding grounds in a long distance migrant

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Abstract

Animals use environmental variables as cues to synchronise the timing of their annual cycle stages to the year-to-year variation in the fitness landscape. However, it has been rarely demonstrated that these cues are indeed predictors for fitness. For migratory birds, male arrival at the breeding grounds is a key decision where the optimal arrival time varies from year-to-year; nevertheless, whether the cues used to time their arrival also predict the conditions at the breeding grounds is largely unknown. We tested which environmental variables explain variation in arrival dates and whether these environmental variables also predict the optimal time to arrive using 11 years from a long-term study population of pied flycatchers. We used a moving climate window approach to test whether temperatures and precipitation from their breeding grounds in the Netherlands and their wintering grounds in the Ivory Coast explained variation in arrival time (*i.e.*, if they are cues). We then tested whether these temperatures also explained optimal arrival time using as fitness measures: the probability of obtaining a female, the number of fledgelings and the probability of producing recruits. Temperature and precipitation in the Netherlands in the month prior to arrival, the temperature in Africa in the month prior to arrival and a lagged precipitation in Africa explained the annual variation of arrival dates. Using the number of fledgelings as fitness measure, the optimal arrival time varied between years and this was correlated with the temperatures in Africa. We conclude that African temperatures are used by pied flycatchers as cues to time their arrival and as predictors for the fitness landscape at the breeding grounds. We further explore whether African temperatures are merely proxies for causal local conditions or if a causal relationship between African temperatures and the fitness landscape exists, discussing the consequences under ongoing climate change.

Introduction

In seasonal habitats, the timing of annual cycle stages, as, for instance, of flowering and bud burst in plants, or reproduction, moult or migration in animals is synchronised with environmental conditions, often with a short window that is optimal for these stages. Organisms living in these seasonal habitats hence need to time their annual cycle stages to occur during this "optimal window", because if the annual cycle stages happen too early or too late, they incur fitness costs. Therefore, the timing of the stages can be under strong stabilising selection. This was largely studied in avian timing of breeding (Perrins 1970; Noordwijk *et al.* 1995; Brown & Brown 2000) and migration (Bêty *et al.* 2004; Smith & Moore 2005), but also in annual cycle stages of fish (Einum & Fleming 2000), plants (Kelly & Levin 1997; Donohue *et al.* 2005; Koenig *et al.* 2012) and invertebrates (Philippart *et al.* 2003).

Optimal time windows may be very narrow in some cases; moreover, they vary in date and/or duration from one year to the other. For instance, the timing of the optimal window may be related to the time when food is abundant (important during the breeding season; Noordwijk *et al*. 1995; Visser *et al*. 2005) or to the optimal weather conditions (important for migration; Brown & Brown 2000; Erni *et al*. 2005). Therefore, individuals need to be able to track the yearly variation of the time optimum and adjust their annual cycle stages accordingly. This, however, is not straightforward because decisions about the timing of stages often have to be made well in advance since many of these stages require preparation (van Noordwijk & Müller 1994; Visser *et al*. 2004, 2010). For instance, to take full advantage of an optimum of food availability during the reproductive stage, a bird must already have chicks to feed. However, having chicks in the nest at this precise moment depends mainly on the decision of when to lay eggs, which happens weeks earlier in the season (Visser 2008, 2013). If these decisions must be made well before the time when selection acts, *i.e.* the optimal window, individuals need to respond to environmental conditions present during the moment of decision-making. This is only possible if the environmental conditions during decision making correlate with or causally affect the fitness landscape (van Noordwijk & Müller 1994; Visser *et al*. 2004). This makes such environmental variable a "cue" (Fig. 4.1).

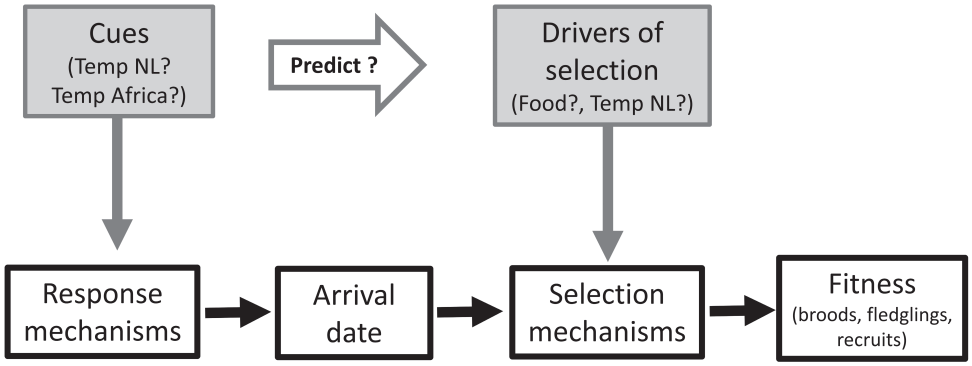

Figure 4.1. Schematic representation of the concepts discussed in the present study. Year-to-year variation in fitness depends on the interaction between the environmental drivers and individual decisions. Because decisions are not made in the same (spatial and temporal) environment of selection, animals use cues to predict conditions of the environment at the time of selection. Adapted from (van Noordwijk & Müller 1994; Visser *et al*. 2004, 2010).

Migratory animals are particularly interesting in this aspect, as their decisions need to be made not only at an earlier time than the optimal time window (time of the optimum in the fitness landscape), but also at a different geographical location, as they breed in a distinct place from where they overwinter. Because long-distance migrants are far away from their breeding grounds, they cannot directly judge the conditions they will face

there upon arrival and during breeding (Both & Visser 2001; Visser & Both 2005). Photoperiodic variation is considered the major cue that these animals use to time their migration (Gwinner & Pévet 1987; Gwinner 1989a, b; Dawson 2002; Coppack & Pulido 2004; Pulido 2007). Nevertheless, photoperiod is invariable among years and thereby it cannot predict annual variation in optimal conditions, making it unreliable to fine tune the timing of migration to the among-year variation in timing of the "optimal window".

Some studies show that fine-tuning of migration timing can be related to environmental conditions (Pulido 2007). For instance, some birds might arrive earlier at their breeding grounds when temperatures are higher before departure (Both *et al*. 2005; Marra *et al*. 2005). Moreover, weather conditions can affect departure decisions (Gordo 2007; Bauer *et al.* 2008; Eikenaar & Schmaljohann 2014; Deppe *et al*. 2015; Ouwehand & Both 2017) and potentially en route decisions as well, leading to small adjustments in timing of spring arrival (Hüppop & Winkel 2006; Bauer *et al*. 2008; Both 2010). Individuals may thus acquire information (*e.g.*, temperature, weather) before and during migration that helps them to predict conditions of the breeding grounds, and thus time their arrival in relation to the optimal window (Bauer *et al*. 2008; Both 2010; Tøttrup *et al*. 2010). It has been demonstrated that conditions that explain variation in avian breeding timing also predict the drivers of selection (Visser *et al*. 2006, 2015), but it is not well known for avian migration timing. This knowledge is relevant in light of current environmental changes. It is known that many bird species have advanced their migration dates, suggesting that migrants are able to track climate change, but this pattern is not consistent across all species (Both & Visser 2001; Cotton 2003; Marra *et al*. 2005; Gienapp *et al*. 2007; Usui *et al*. 2016). However, whether these changes track shifts in optimal conditions is not well known (Visser & Both 2005). If the cues the animals use for timing their migration merely correlate with the drivers of selection, without causally affecting the fitness landscape, unequal effects of climate change in time and space will decrease the reliability of these cues in the future.

To understand which environmental variables could serve as cues for the timing of arrival of migratory birds, we analysed 11 years of data on individual arrival time and breeding success of a long distance migratory passerine, the European pied flycatcher (*Ficedula hypoleuca*). We identified temperature or precipitation variables that males use as cues to time their arrival at the breeding grounds and tested whether these variables predict the optimal time of arrival (*i.e*. the fitness landscape).

Methods

Study system and study area

Pied flycatchers (*Ficedula hypoleuca* ([Pallas], 1764); Muscicapidae) are small long-

distance migratory birds that breed in Europe and winter in Africa. Due to their propensity to use nest boxes, they also allow breeding to be precisely monitored. Long-term data collection was conducted in the forests of the Hoge Veluwe National Park (The Netherlands; 52°02'07"N 5°51'32"E). Forested areas in the park are dominated by pedunculate oaks (*Quercus robur*), northern red oaks (*Quercus rubra*), Scots pines (*Pinus sylvestris*), larches (*Larix* spp.) and birches (*Betula* spp.). We provide around 400 nest boxes year-round in an area of 171 ha which are occupied in spring by cavity-nesters such as pied flycatchers, great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), nuthatches (*Sitta europaea*) and coal tits (*Periparus ater*). Voucher material of this pied flycatcher population was deposited in the ornithology collection of the Naturalis Biodiversity Center (Leiden, The Netherlands) under the inventory numbers RMNH 592347, RMNH 592348 and RMNH 592349.

Male arrival dates

Male individual arrival data were collected from 2005 to 2015 (11 years). Individual arrival date of males was assessed by daily scoring newly arriving males in our study area from early April (Visser *et al*. 2015; see also Both *et al*. 2016; Potti 1998). Birds choose a territory upon arrival and advertise their cavity or nest box to the females by singing continuously at or close to the potential nest site. Two or three trained observers walked independently pre-established routes covering the whole study area and visiting all boxes. Routes and direction of the routes were alternated daily among observers in order to prevent biases due to among-observer variation in detection probability and accuracy. Detected birds were described in terms of plumage and aluminium/colour ring combinations. Male pied flycatchers in the Netherlands display relatively large individual variation in plumage characteristics which, combined with colour ring combinations, allows an initial recognition of an individual in the field without the need of capturing the birds. In our study site, plumage coloration varied from female-brown or light grey to almost entirely black and white with intermediates of increasing blackness (Drost 1936). The white forehead patch also varied in size, from absent to a large patch covering most of the forehead, and also in shape from two distinct dots to a rectangular-shaped patch (Lundberg & Alatalo 1992). We associated singing males to the closest nest-box in the vicinity. During chick-rearing phase (see below), males were caught and described again in terms of plumage characteristics and ring combination. In most years (not in 2005 and 2012) we also collected data on "bachelors", *i.e*. males that are not paired when most females had arrived. Those males were captured and identified when they were inspecting and advertising their potential nest site using spring traps installed at the entrance of the nest boxes. Some of those presumed bachelors became breeding birds later in the season.

Individual breeding success

Apart from data on timing of arrival, we also collected information on individual breeding success using our standardised nest monitoring protocol. For all years in which we had arrival data we collected data on whether the male obtained a female or not (as described above), female egg-laying dates, clutch size, brood size, number of chicks successfully raised (*i.e.* number of fledglings) and whether individual offspring recruited as a breeding bird (a so-called recruit) in the following year(s) or not. We only included first broods, however, in the few cases of polygyny in which males had females with similar laying dates, both broods were included.

Environmental variables

Data on daily environmental variables was obtained from the Dutch meteorological institute database (KNMI - https://www.knmi.nl/nederland-nu/klimatologie/, accessed in February 2016) for the Netherlands temperatures and precipitation and from the US National Oceanic and Atmospheric Administration database (NOAA - ftp://ftp.ncdc.noaa.gov/pub/data/gsod/, February 2016) for African temperatures and precipitation. Data from the NOAA database was converted to match the KNMI database so all values in Fahrenheit were converted to Celsius for temperatures and inches to mm for precipitation.

For the Dutch environmental variables, we used data from the Deelen weather station which is directly adjacent to the study area. To select the station for the African temperature data, we used information of pied flycatchers' wintering location previously reported from geolocator data (Ouwehand *et al.* 2016) to identify the closest weather station to the wintering grounds. According to this data, pied flycatchers from the Netherlands winter in the Ivory Coast, where Daloa (6°27'W 6°53'N) was the closest weather station with a reasonable amount of data to be used. Because the dataset still had large gaps, we also used information from two other nearby locations (Gagnoa, 5°56'W 6°08'N, and Yammousoukro, 5°17'W 6°49'N). To fill the remaining few gaps in the data, we interpolated the missing data. We did not expect this procedure to have an undue impact due to the way this data is used in the statistical analysis (see below on "Causes of arrival").

We also obtained data on the photoperiodic variation of the Netherlands from the NOAA. We considered the civil twilight as the boundary of the effective light phase important for the birds following Gwinner (1989a). Because photoperiodic variation is completely correlated throughout all locations of the Earth, it was not necessary to obtain and model day length data for Africa separately.

Data analysis

All analyses were performed in R version 3.2.1 (R Core Team 2015). To define the minimal adequate models, we used backwards model selection, *i.e.* sequentially dropping non-significant terms starting with interactions.

We had too few individuals with repeated observations of arrival dates (out of 477 individuals, only 140, 29%, had more than one observation) for using a mixed effect model without model convergence issues. We thus decided to retain only a single observation per individual in the dataset, excluding any other repeated observation(s). The retained observation was randomly selected.

a) Causes of arrival

Following the method described in Gienapp *et al.* (2005) we used proportional hazard models (Cox 1992) implement in the R "survival" package (Therneau 2015). Proportional hazard models calculate the daily probability of an event to occur. They, therefore, allow including time-dependent variables, *i.e.* variables that change their value during the time an individual is "at risk". Modelling effects of weather variables on annual cycle stages, as arrival time, is biologically more realistic than using fixed time windows over which these variables are averaged (Gienapp *et al.* 2005). The value of this time-dependent weather variable at day t was calculated as the average over periods of various lengths (5 to 30 days) ending at day t. For African weather variables, we also used lagged shifting windows of the same length (20 days) but ending 20 to 80 days before day t (based on the time taken during spring migration, Ouwehand *et al.* 2016). In total, we compared 24 possible combinations (see Supplementary material, Table S4.1). We then tested, also with proportional hazard models, which variables significantly explained the variation in arrival time of the pied flycatchers. We fitted African (with and without lag) and Dutch temperatures, African (with and without lag) and Dutch precipitation and the two-way interactions between day length and Dutch temperature and day length and African temperature (with lag). In this analysis we also included characteristics of the birds that could potentially explain variation in arrival dates: the Drost score (variation in male colour from 0 completely black males to 7 brown males; Drost 1936) and age (2nd-calendar-year birds, birds that hatched the year before; after second-calendar-year-birds, birds that lived more than two calendar years and unknown. Given the difficulties of ageing the birds based on plumage characteristics, this last age category was assigned to birds not born in the study area during the first year we recorded them breeding.

Finally, we tested with simple regressions how the temperatures included in the best model were correlated (*i.e.*, Dutch temperatures prior to arrival, African temperatures prior to arrival and African temperatures with lag) and whether they changed over time (regression against year as a continuous variable).

b) Consequences of arrival

We tested whether male fitness depended on arrival time and also if this relationship differed among years. To test whether the peak in the fitness landscape for arrival date, shifted from year to year, we regressed fitness against arrival date and arrival date squared, both in interaction with year. The interaction of arrival date and year in the quadratic regression indicates the date of arrival for maximal fitness in that year, thereby, it tests the year-to-year shifts in the optimal time. We used several fitness components for this analysis: the probability of attracting a female and reproducing, number of fledgelings and the probability of producing recruiting offspring. Sample sizes varied depending on whether the variable could have been affected by an experiment (performed in some of the years for which we had data available) such as data on fledgelings and recruits and whether or not they were collected in all years (such as the probability of obtaining a female). We then tested how different environmental variables predicted the fitness landscapes of males by replacing year in the above-explained analysis by the environmental variable. In all cases, the tests were done with generalised linear mixed models with year as a random effect for each environmental variable separately. We used a logit-link and Binomial error distribution for the probability of obtaining a female and recruits and normal distribution the number of fledgelings. As environmental variables, we used the average Dutch and African temperatures that best explained the variation in arrival dates for each individual (these were the same temperatures defined as the best predictors for arrival and calculated with the proportional hazards model as explained above).

We also explored whether African temperatures are a proxy for local conditions that determine the fitness landscape. We first explored which local environmental variables explained optimal arrival time by fitting their interaction with arrival time in mixed models with number of fledgelings as dependent variable, analogous to the models described above. We used similar local environmental variables as those used in Visser *et al*. (2015): the annual food peak date, the annual food peak height, the annual mismatch between mean egg-laying dates and food peak date, the temperatures when chicks were in the nest (nestling temperatures, calculated for each year by averaging temperatures from [mean egg-laying date plus 6 days of egg laying, plus 12 days of incubation] to [egg-laying date plus the 18 days of egg-laying and incubation, plus 12 days of chick rearing]) and the temperatures when chicks had fledged but were still receiving parental care (the fledgeling temperatures, calculated for each year by averaging temperatures from [egg-laying date plus the 30 days of egg-laying, incubation and chick rearing] to [egg-laying date plus 30 days of egg-laying, incubation and chick rearing, plus 12 days of post-fledgling care]). If these local variables are the causal drivers of optimal arrival time, they should be better predictors of optimal arrival time than African temperatures. Thus, this could be tested by running subsequent models including both the African

temperatures and the significant local environmental variables, both in interaction with arrival time.

Results

Also see the Supplementary material for the Tables with the complete results of the model selection and statistical analyses.

Causes of arrival date

Variation of male arrival correlated with Dutch and African temperatures in the month prior to arrival as well as with Dutch precipitation prior to arrival and African precipitation with the window moved by an 80-day lag (thus starting, on average, around the 29th of January, Table S4.1). The duration of the window for African and Dutch temperatures as well as for the Dutch precipitation was found to be 30 days (Table S4.1) while the duration of the lagged window was set at 20 days as explained before. Higher temperatures in the Netherlands were related to earlier arrival; with a significant interaction between temperature and day length: the temperature effect was weaker later in the season (coefficient for the interaction = -0.01, coefficient for temperature = 5.38, χ^2 = 27.98, *p*-value <0.01, Table S4.2). African temperatures prior to arrival were related to arrival dates in the opposite direction, with higher temperatures related to late arrival (regression coefficient = -0.43, χ^2 = 25.38, *p*-value <0.01, Supplementary material, Table S4.2, Fig. S4.1). Finally, higher precipitation in the Netherlands were related to later arrival (coefficient = -0.28, χ^2 = 37.78, *p*-value <0.01, Table S4.2), but higher African precipitation values with lag predicted earlier arrival (coefficient = 3.14, χ^2 = 6.62, *p*-value = 0.01, Table S4.2). Neither African temperatures earlier in the year (African temperatures with lag) nor precipitations in Africa prior to arrival explained variation in arrival dates (Table S4.2).

Male arrival was also significantly explained by individual age and colour. After second calendar year males tended to arrive earlier than second calendar year birds (coefficient for younger = - 0.78, χ^2 = 27.06, *p*-value <0.01, Table S4.2) and darker males (lower Drost scores) tended to arrive earlier than brown males (higher Drost scores) (coefficient = - 0.22, χ^2 = 15.08, *p*-value <0.01, Table S4.2).

There was no correlation between any of the African and the Dutch temperatures, but lagged African temperatures were significantly related to African temperatures prior to arrival (slope = 0.49 ±0.18, $F_{1,9}$ = 7.46, *p*-value = 0.02; Supplementary material, Table S4.3, Fig. S4.2).

Consequences of arrival date

There was a significant relationship between the probability of obtaining a female and arrival date of the male (with a significant quadratic term for arrival date). Late arriving males had a much lower probability of obtaining a female than early arriving males (quadratic estimate = -0.01 ±0.004, linear estimate = 0.15 ±0.15, χ^2 = 3.92, n = 408, *p*-value quadratic term = 0.05, Table S4.4). This probability, however, did not differ among years (Fig. 4.2, Table S4.4).

The number of fledgelings generally declined with arrival date but peaked in the first third of the arrival dates (significant quadratic term for arrival date, estimate = -0.01 ±0.005, $F_{1,269}$ = 8.25, *p*-value <0.01). The location of this peak varied from year to year (explained by the interaction between male arrival date and year, $F_{1,260}$ = 1.92, *p*-value = 0.05, Table S4.4, Fig. 4.2).

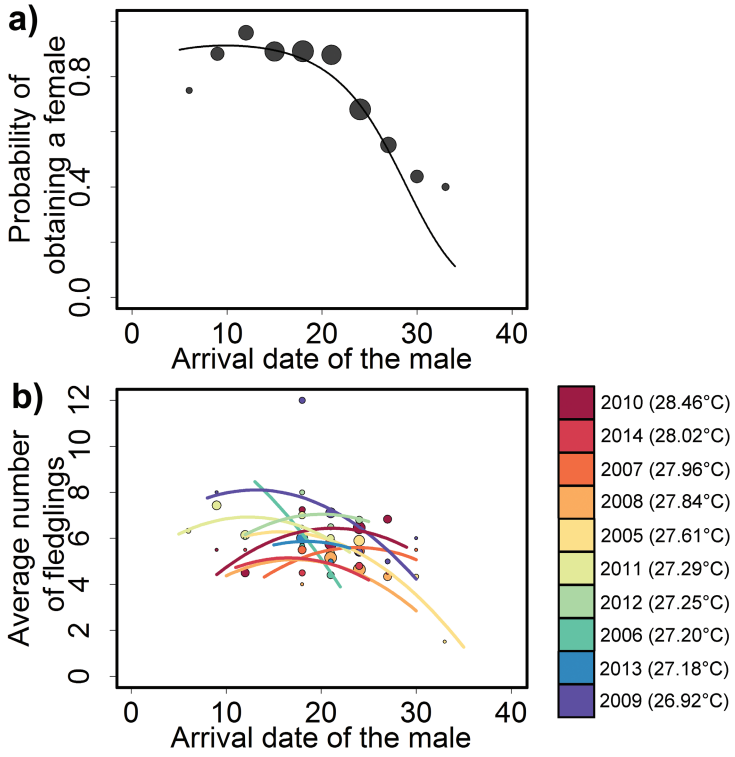

Figure 4.2. a) Probability of obtaining a female and **b)** average number of fledgelings in relation to the arrival date of the male (in April days). Points correspond to the average probability of obtaining a female or mean number of fledgelings for all males that arrived in each of the 5 day-bins starting from April day 0 (= 31st of March). Colours in plot b represent different years and are ordered in the legend by the average African temperatures in the month preceding arrival (warmest to coldest). Size of the symbols represent sample sizes: **a)** largest = 92, smallest = 4, **b)** largest = 14, smallest = 1.

Finally, the probability of producing a recruiting offspring was not significantly related to neither male arrival date nor the year (Fig. 4.2).

From all environmental variables that we tested as predictors of the fitness landscape of males, only the African temperatures immediately prior to arrival ($F_{1, 253.71} = 6.49$, p-value = 0.01, Table S4.5) and African temperatures earlier in the year ($F_{1, 253.86} = 5.39$, p-value = 0.02, Table S4.5) predicted the date of the fitness peak. None of the local variables was significant and also did not explain the other fitness components analysed (*i.e.* the probability of breeding and of producing recruits). Thus, even if all local predictors were tested in the same model with the African temperatures prior to arrival, only the African temperature remained as a significant predictor ($F_{1, 274.92} = 9.34$, p-value <0.01, Table S4.6).

Discussion

Temperature and precipitation in the Netherlands during arrival and African temperature in the month prior to arrival, but not African temperature in January-February (with 80-day lag), explained year-to-year variation in timing of arrival at the breeding grounds. The same African temperatures also explained year-to-year variation in optimal arrival date, *i.e.* the peak of the fitness landscape. These results suggest that African temperatures are cues for the pied flycatchers to time their arrival and that this cue is adaptive as African temperatures are related to the fitness landscape at the breeding grounds (see also Supplementary material, Fig. S4.3).

It has been previously shown that temperature, both en route and of the breeding grounds, predicts variation in timing of spring arrival, or, at least, the timing of passage dates in the pied flycatcher and other passerines (Saino *et al.* 2007). An interesting question arising from these results is why temperatures in Africa would predict fitness landscapes in the European breeding grounds. We can imagine at least three possible reasons: **(a)** correlation between environmental conditions in the Netherlands and Africa; **(b)** an effect that arises via females instead of males; **(c)** phenology and fitness are causally determined by African temperatures, for instance, via body/physiological conditions of males (Fig. 4.3). We explore these potential causes below, but it is important to stress that, for the moment, most explanations remain speculative.

(a) The existence of large-scale correlations in climatic conditions between the Netherlands and Africa would potentially allow birds to predict the conditions at the breeding grounds using the temperatures in their wintering grounds (Fig. 4.3a). A few studies suggest that this could be possible and that at least some aspects of the climate are correlated between Europe and Africa (*e.g.*, Lehikoinen *et al.* 2004; Saino & Ambrosini 2008). Moreover, it would still be possible that different (and more

important) conditions are correlated with African temperatures, such as temperatures that predict a food peak at the breeding grounds. Our additional analyses, however, showed that none of the local environmental variables tested explained the variation in fitness. Thus, the African temperatures prior to arrival are better predictors of the fitness landscape than the environmental variables of the breeding grounds. This argues against the hypothesis that African temperatures affect the fitness landscape via a correlation with the environmental variables at the breeding grounds.

(b) While our analysis only takes males into account, it is possible that the fitness landscape at the breeding grounds is related to the arrival date of females (Fig. 4.3b). For example, the fitness of the male could be related to both the availability and reproductive success of females; these conditions, in turn, could be correlated to African temperatures. It is interesting to notice that while female fitness peaks may depend on the same temperatures affecting males (or some correlated variables), the probability of a male to reproduce (directly related to the female availability) is not dependent on African temperatures (Fig. 4.2a). This probability is, instead, exclusively driven by male arrival: males that arrive early will always be more likely to obtain a female. In our population, female arrival date is significantly related to male arrival date, with early males having a higher probability of mating with early arriving and early laying females. However, this relation is fairly weak and for a large number of males arriving early is no guarantee of breeding early (Supplementary material part 3, Table S4.7). Thus, the gain of male fitness with early arrival via female earliness, as observed in other studies (Saino *et al*. 2004; Cooper *et al*. 2010), is not so straightforward (see also Both *et al*. 2016; Chapter 5).

(c) The African temperatures could also directly affect the conditions of the birds upon arrival (Fig. 4.3c), which in turn would shape the year-to-year variation in fitness landscapes. For example, if individuals tend to arrive in poorer body conditions in some years, they could be "constrained" to breed later (Perrins 1970; Visser *et al*. 2012). This is a common situation for non-passerine migrants, such as some geese species, which heavily depends on their body reserves upon arrival to breed early (van der Jeugd *et al*. 2009). Early breeding in suboptimal conditions is costly, as egg formation and, later, chick rearing are energetically expensive activities (Visser & Lessells 2001). In the case of males, this cost could be related to defending a territory and attracting a female. Saino *et al*. (2004) support a more direct relation between conditions important for arrival and fitness in the form of a carry-over effect. According to Saino *et al*. (2004), good winter conditions (NDVI) predicted earlier arrival dates of barn swallows (*Hirundo rustica*), which in turn predicted earlier breeding and a higher probability of second broods. In this case, it is less clear whether the conditions from the wintering grounds serve as a cue for earlier breeding or acts as a constraint that prevents earlier arrival and breeding. Pied flycatchers perform a partial moult in their breeding grounds before migrating to their

wintering grounds. In this moult the males gain the plumage that will be important for breeding as females may select males based on plumage quality and ornaments (Galván & Moreno 2009; Sirkiä & Laaksonen 2009; Canal *et al*. 2011). If conditions in Africa affect this moult, the effects could carry-over to the breeding grounds (Hedenström *et al*. 2007; Hera *et al*. 2013).

For African temperatures to directly affect individuals, they must be related to food availability or some other condition in the wintering grounds that will affect the accumulation of reserves by the individuals. Timing of migration may indeed be dependent on the individual condition due to carry-over effects from good wintering habitats (Norris *et al*. 2004; Saino *et al*. 2004; Pulido 2007; Studds & Marra 2011). For example, Tøttrup *et al*. (2012) reported that droughts in the wintering grounds caused delays in arrival time of songbirds; the reason for this was a prolonged stay in stopover sites, suggesting that these birds had a slower fueling rate. Our additional analyses support that conditions in Africa are more important in determining optimal arrival time than conditions of the breeding grounds, but unfortunately, at the present, we do not know the exact mechanism.

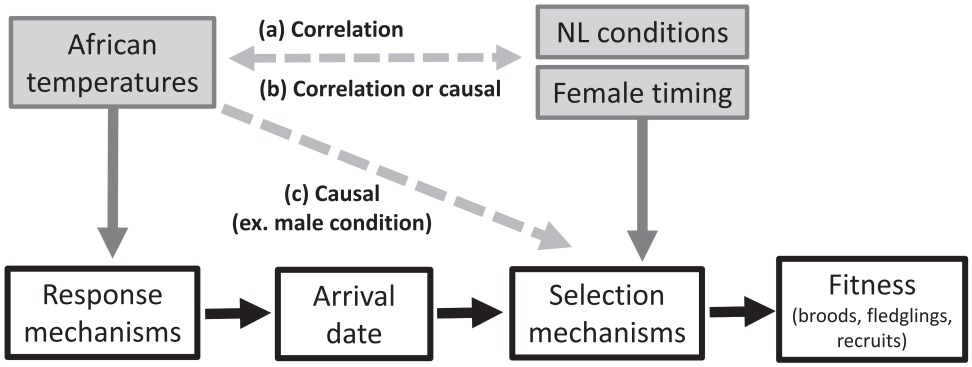

Figure 4.3. A few of the possible scenarios explaining why African temperatures would correlate with fitness at the breeding grounds: **a)** via correlation with conditions of the breeding grounds; **b)** via correlation with the something that determines female timing or **c)** African temperatures causally affects the fitness landscapes, for example, via male condition.

Climate change leads to increased temperatures, but not in a uniform manner across different regions and moments of the year (Easterling *et al*. 1997; Vose *et al*. 2005; Serreze & Francis 2006). If the use of African temperatures as a cue corresponds to a mere correlation between conditions of the breeding and wintering grounds, because climate change does not necessarily affect African and Dutch temperatures in the same way, the use of African temperatures as cues may actually become unreliable in the near future, with potential consequences for population demographic processes. However, if there is indeed a causal effect of the African temperatures on the fitness parameters

(for example, due to an effect on the bird's condition that carries over to the breeding grounds), as our data support, unequal changes caused by climate change will not affect the relevance of African temperatures for timing of migration – as the change in conditions in one part of the world will be accompanied by a changes in fitness in the location in which selection takes place.

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Supplementary material

Additional figures and tables

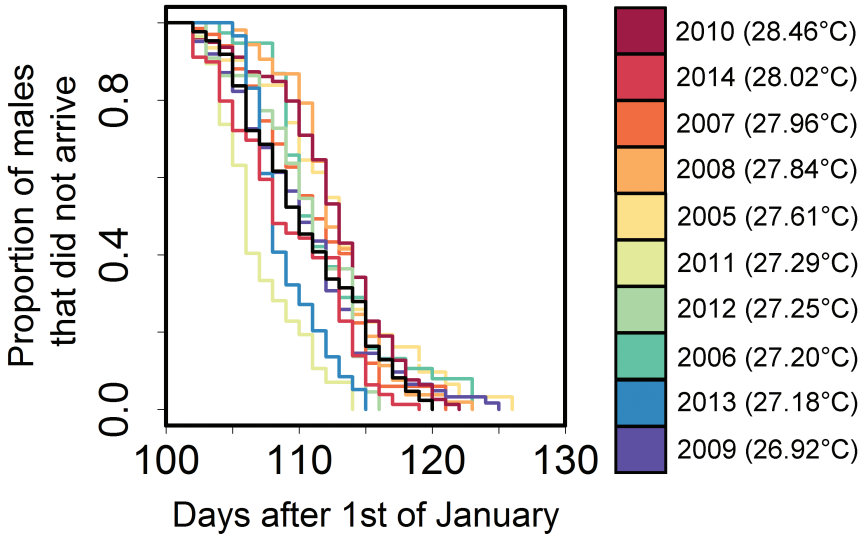

Figure S4.1. Proportion of males that did not arrive in relation to days since 1st of January. Different coloured lines in the graph represent different years, temperatures represent the African temperatures in the month prior to arrival.

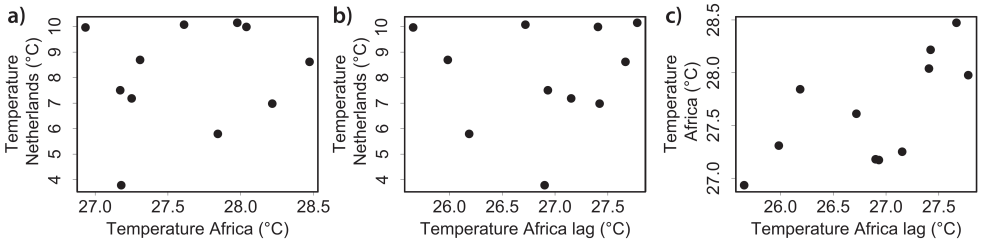

Figure S4.2. Correlations between mean annual **a)** African (without lag) and Dutch temperatures, **b)** African (with lag) and Dutch temperatures and **c)** African (without lag) and African (with lag) temperatures, using the best intervals defined in the model from Table S4.1.

Table S4.1. Log-likelihood used in the model selection of all models for male arrival date. Models differ in the length of the temperature window (in days) for African and Dutch temperatures prior to the event or in the position of the window (lag in days) for the African temperature (with a fixed window of 20 days). The value in bold corresponds to the best model fit.

Window duration evaluated for temperatures without lag (days)	Lag for African temperatures (days), with window of 20 day-duration	Model Log Likelihood	Order
5	20	-3707.27	22
5	40	-3702.54	15
5	60	-3705.23	19
5	80	-3439.94	5
10	20	-3702.76	17
10	40	-3700.91	14
10	60	-3705.48	20
10	80	-3430.67	4
15	20	-3698.63	12
15	40	-3696.29	11
15	60	-3706.83	21
15	80	-3424.62	2
20	20	-3708.19	23
20	40	-3703.42	18
20	60	-3713.66	24
20	80	-3440.55	6
25	20	-3698.88	13
25	40	-3694.09	10
25	60	-3702.64	16
25	80	-3429.02	3
30	20	-3690.36	8
30	40	-3685.86	7
30	60	-3691.95	9
30	**80**	**-3420.31**	**1**

Table S4.2. Model results for the effects of temperatures on the timing of stages analysed with proportional hazard models. Statistics are given for each term at the point of exclusion of the term from the model. Coefficients are presented only for significant terms or main terms in the presence of significant interactions.

Arrival date (with preciptation and temperature)	**Coefficient**	**Events**	χ^2	***p*-value**
Day length : Temperature NL	-0.01	633	27.98	**<0.01***
Day length : Temperature Africa (lag)		633	2.68	0.10
Temperature Netherlands (30 days period, no lag)	5.38	633		
Temperature Ivory Coast (30 days period, no lag)	-0.43	633	25.38	**<0.01***
Temperature Ivory Coast (20 days period, 80 days lag)		633	0.10	0.75
Preciptation Netherlands (30 days period, no lag)	-0.36	633	44.13	**<0.01***
Preciptation Ivory Coast (30 days period, no lag)		633	1.17	0.28
Preciptation Ivory Coast (20 days period, 80 days lag)	3.14	633	6.62	**0.01***
Drost score	-0.07	633	15.08	**<0.01***
Male age (unknown)	-0.22	633	27.06	**<0.01***
Male age (young)	-0.78			

Table S4.3. Model results for the relation between Dutch and African temperatures. Statistics are given for each term at the point of exclusion of the term from the model. Estimates and standard errors are presented only for significant terms.

Temperature Netherlands	**Estimates**	**s.e.**	**ndf**	**ddf**	**R^2 (adjusted)**	***F*-test**	***p*-value**
Temperature Africa			1	9	-0.08	0.29	0.61
Temperature Africa (80-days lag)			1	9	-0.11	0.02	0.88
Year			1	9	0.02	1.17	0.31
Temperature Africa	**Estimates**	**s.e.**	**ndf**	**ddf**	**R^2 (adjusted)**	***F*-test**	***p*-value**
Temperature Africa (80-days lag)	0.49	0.18	1	9	0.39	7.46	**0.02***
Year			1	9	-0.07	0.37	0.56
Temperature Africa lag	**Estimates**	**s.e.**	**ndf**	**ddf**	**R^2 (adjusted)**	***F*-test**	***p*-value**
Year			1	9	-0.06	0.45	0.52

Table S4.4. Model results for the multiple regression analyses testing the effects of arrival date and year on different fitness components. Statistics are given for each term at the point of exclusion of the term from the model. Estimates and standard errors are presented only for significant terms.

Probability of obtaining a brood	**Estimates**	**s.e.**	**df**	**sample**	χ^2	***p*-value**
Arrival date^2 : Year			7	408	10.98	0.14
Arrival date : Year			7	408	5.98	0.54
Arrival date^2	-0.01	0.004	1	408	3.92	**0.05**
Arrival date	0.15	0.15	1	408		
Year			7	408	9.28	0.23
Number of fledglings	**Estimates**	**s.e.**	**ndf**	**ddf**	***F*-test**	***p*-value**
Arrival date^2 : Year			9	251	0.38	0.95
Arrival date : Year			9	260	1.92	**0.05**
Arrival date^2			1	269	8.25	**<0.01***
Arrival date : Year (2005)	0.43	0.22				
Arrival date : Year (2006)	-0.03	0.29				
Arrival date : Year (2007)	0.64	0.22				
Arrival date : Year (2008)	0.47	0.21				
Arrival date : Year (2009)	0.35	0.19				
Arrival date : Year (2010)	0.57	0.18				
Arrival date : Year (2011)	0.34	0.15				
Arrival date : Year (2012)	0.55	0.21				
Arrival date : Year (2013)	0.50	0.27				
Arrival date : Year (2014)	0.45	0.21				
Arrival date^2	-0.01	0.005				
Year (2005)	2.92	2.76				
Year (2006)	11.20	4.63				
Year (2007)	-2.05	2.86				
Year (2008)	1.06	2.62				
Year (2009)	5.78	2.01				
Year (2010)	0.35	1.80				
Year (2011)	4.85	1.30				
Year (2012)	1.57	2.92				
Year (2013)	1.29	3.94				
Year (2014)	1.44	2.76				
Probability of obtaining recruits	**Estimates**	**s.e.**	**df**	**sample**	χ^2	***p*-value**
Arrival date^2 : Year			7	249	6.49	0.48
Arrival date : Year			7	249	10.00	0.19
Arrival date^2			1	249	3.04	0.08
Arrival date			1	249	0.30	0.59
Year			7	249	7.44	0.38

Table S4.5. Environmental variables potentially affecting selection on arrival date in pied flycatchers (tested separately).

	Probability of obtaining a brood					Number of fledglings					Probability of obtaining recruits				
Temperature Netherlands migration	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**	**Estimate**	**s.e.**	**ddf**	***F*-test**	***p*-value**	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**
Arrival : Temp NL	0.03	0.02	3	2.00	0.14	-0.01	0.02	237.07	0.08	0.78	-0.01	0.02	3	-0.30	0.78
Temperature Africa migration	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**	**Estimate**	**s.e.**	**ddf**	***F*-test**	***p*-value**	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**
Arrival : Temp Africa	-0.07	0.06	3	-1.17	0.33	0.16	0.06	253.71	6.49	**0.01***	0.13	0.07	3	1.83	0.16
Temperature Africa lag migration	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**	**Estimate**	**s.e.**	**ddf**	***F*-test**	***p*-value**	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**
Arrival : Temp Africa Lag	-0.07	0.04	3	-1.67	0.19	0.09	0.04	253.86	5.39	**0.02***	0.03	0.04	3	0.65	0.56
Preciptation Netherlands migration	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**	**Estimate**	**s.e.**	**ddf**	***F*-test**	***p*-value**	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**
Arrival : Prec NL	0.01	0.04	3	0.19	0.86	-0.26	0.19	236.98	1.93	0.17	-0.07	0.04	3	-1.69	0.19
Preciptation Africa migration	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**	**Estimate**	**s.e.**	**ddf**	***F*-test**	***p*-value**	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**
Arrival : Prec Africa	0.04	0.02	3	2.13	0.12	-0.12	0.08	250.96	2.12	0.15	-0.05	0.02	3	-2.50	0.09
Preciptation Africa lag migration	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**	**Estimate**	**s.e.**	**ddf**	***F*-test**	***p*-value**	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**
Arrival : Prec Africa Lag	0.19	0.69	3	0.28	0.80	0.33	2.41	250.74	0.02	0.89	-1.28	1.09	3	-1.17	0.33
Food peak date	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**	**Estimate**	**s.e.**	**ddf**	***F*-test**	***p*-value**	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**
Arrival : Food peak date	-0.002	0.003	3	-0.53	0.64	0.01	0.003	272.65	2.31	0.13	-0.001	0.003	3	-0.25	0.82
Food peak height	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**	**Estimate**	**s.e.**	**ddf**	***F*-test**	***p*-value**	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**
Arrival : Food peak height	0.002	0.001	3	2.04	0.64	-0.001	0.001	275.97	0.24	0.63	-0.001	0.001	3	-0.75	0.51
Mismatch	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**	**Estimate**	**s.e.**	**ddf**	***F*-test**	***p*-value**	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**
Arrival : Mismatch	0.002	0.004	3	0.49	0.66	-0.01	0.004	275.87	2.89	0.09	0.0003	0.004	3	0.09	0.93
Mean nestling temperature	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**	**Estimate**	**s.e.**	**ddf**	***F*-test**	***p*-value**	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**
Arrival : Nestling Temp	0.01	0.03	3	0.57	0.61	-0.02	0.02	275.86	0.93	0.34	0.002	0.02	3	0.08	0.94
Mean fledgling temperature	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**	**Estimate**	**s.e.**	**ddf**	***F*-test**	***p*-value**	**Estimate**	**s.e.**	**df**	***t*-statistic**	***p*-value**
Arrival : Fledgling Temp	-0.02	0.02	3	-0.88	0.44	0.04	0.02	272.97	2.94	0.09	0.04	0.02	3	1.86	0.16

Table S4.6. Model results for the multiple regression analyses testing the number of fledglings in relation to the African temperature prior to arrival and the local environmental factors in the same model.

Number of fledglings	Estimates	s.e.	ndf	ddf	*F*-test	*p*-value
Temperature A (no lag) : Arrival date	0.16	0.06	1	253.71	6.49	**0.01***
Food peak height : Arrival date			1	243.80	0.07	0.79
Food peak date : Arrival date			1	245.18	0.02	0.88
Temperatures nestling : Arrival date			1	240.17	0.69	0.41
Temperatures fledgling : Arrival date			1	247.63	0.18	0.67
Arrival date^2	-0.01	0.005	1	253.63	4.58	**0.03***
Food peak height			1	6.12	2.13	0.19
Food peak date			1	4.27	0.05	0.83
Temperatures nestling			1	5.58	1.84	0.23
Temperatures fledgling			1	5.19	0.43	0.54

Reaction norms

Our results suggest that there is potential for the pied flycatchers to track changes in temperatures (in Africa) and adequately time their arrival at the breeding grounds. Interestingly, the relation between fitness and temperature is steeper than one between arrival dates and temperature (Fig. S4.3). This suggests that the optimal arrival time responds more strongly to the temperature than the trait arrival date when temperatures increase. This follows the expectations of Gienapp *et al.* (2014) who suggested that the trait ("consumer") reaction norm is always flatter (less plastic) than the optimal time ("resource", which is unknown in this case) reaction norm because the cue does not perfectly predict the fitness landscape. As a consequence, even if the temperatures affecting "consumer" and "resource" (or breeding and wintering grounds) change equally, there will be selection on the trait (Gienapp *et al.* 2014).

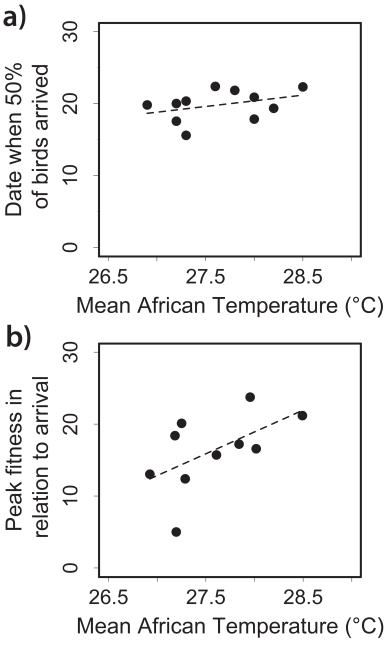

Figure S4.3. a) Date when 50% of birds arrived in relation to the mean African temperature. **b)** Peak date of fitness (of arrival date) in relation to the mean African temperature. The points in these two figures do not correspond to raw data. In Fig. S4.3a they are estimates from a proportional hazards model of the day when 50% of the individuals arrived in each year (from model of Fig. S4.1.). In Fig. S4.3b they are estimates from a linear mixed effect model of the day when the curves peak in each year (from model of Fig. 4.2b).

Consequences of arrival date - Females

We used data on nest building as a proxy for female arrival date, following the same procedure of Visser *et al.* (2015), we had individual pied flycatcher nest building data from our study area from 1980 to 2015, allowing the observation of long-term trends of arrival dates of females. Pied flycatcher female nest building reflects the arrival data of the females since females immediately choose a male and start nest building shortly after arriving (Dale *et al.* 1992, Dale & Slagsvold 1995, Visser *et al.* 2015). However, this data is also highly correlated with egg-laying dates, as expected.

Arrival date of females was significantly related with the arrival date of the male (estimate ±s.e. = 0.89 ±0.13; R-squared = 0.23; $F_{1,164}$ = 50.55; *p*-value <0.01, Table S4.7). Female arrival date also significantly explained the average number of fledglings ($F_{33,743}$ = 1.91; *p*-value <0.01) and chick recruitment probability (χ^2 = 43.68; *p*-value = 0.04), with early females having a higher fitness (Tables S4.8, S4.9). In both cases we observed significant additive year effects but no significant interactions between year and arrival (Tables S4.8, S4.9).

Table S4.7. Model results for the multiple regression analyses testing the relation between arrival date of females and males. Statistics are given for each term at the point of exclusion of the term from the model. Estimates and standard errors are presented only for significant terms.

Female arrival date	**Estimates**	**s.e.**	**ndf**	**ddf**	**R^2 (adjusted)**	***F*-test**	***p*-value**
Male arrival date : Year			10	144	0.30	0.65	0.77
Male arrival date			1	154	0.32	51.22	**<0.01***
Year			10	154	0.32	2.14	**0.02***
Male arrival date	0.91	0.13					
Year (2005)	9.33	4.26					
Year (2006)	5.46	4.41					
Year (2007)	6.16	3.79					
Year (2008)	8.09	4.04					
Year (2009)	11.91	3.41					
Year (2010)	12.41	3.13					
Year (2011)	7.97	2.49					
Year (2012)	6.12	3.71					
Year (2013)	7.42	2.54					
Year (2014)	13.46	2.66					
Year (2015)	10.45	2.49					

Table S4.8. Estimates and standard errors for the multiple regression analyses testing the effects of arrival date of the female and year on number of fledgelings.

Number of fledglings	Estimates	s.e.
Arrival date^2 : Year (1980)	-0.01	0.004
Arrival date^2 : Year (1981)	-0.01	0.002
Arrival date^2 : Year (1982)	-0.004	0.01
Arrival date^2 : Year (1983)	-0.004	0.01
Arrival date^2 : Year (1984)	-0.002	0.002
Arrival date^2 : Year (1985)	-0.001	0.003
Arrival date^2 : Year (1986)	0.01	0.01
Arrival date^2 : Year (1987)	-0.001	0.002
Arrival date^2 : Year (1988)	-0.002	0.003
Arrival date^2 : Year (1989)	0.004	0.003
Arrival date^2 : Year (1990)	0.002	0.01
Arrival date^2 : Year (1991)	0.002	0.004
Arrival date^2 : Year (1992)	-0.01	0.01
Arrival date^2 : Year (1993)	-0.01	0.01
Arrival date^2 : Year (1994)	-0.01	0.01
Arrival date^2 : Year (1995)	0.001	0.001
Arrival date^2 : Year (1996)	-0.01	0.01
Arrival date^2 : Year (1997)	0.001	0.003
Arrival date^2 : Year (1998)	-0.001	0.01
Arrival date^2 : Year (1999)	0.01	0.01
Arrival date^2 : Year (2000)	0.004	0.01
Arrival date^2 : Year (2001)	-0.01	0.04
Arrival date^2 : Year (2002)	0.004	0.02
Arrival date^2 : Year (2003)	-0.23	0.05
Arrival date^2 : Year (2004)	0.004	0.02
Arrival date^2 : Year (2005)	-0.004	0.004
Arrival date^2 : Year (2006)	0.02	0.01
Arrival date^2 : Year (2007)	-0.004	0.01
Arrival date^2 : Year (2008)	0.04	0.02
Arrival date^2 : Year (2009)	-0.003	0.002
Arrival date^2 : Year (2010)	-0.001	0.003
Arrival date^2 : Year (2011)	-0.003	0.002
Arrival date^2 : Year (2012)	0.000	0.004
Arrival date^2 : Year (2013)	-0.004	0.002
Arrival date^2 : Year (2014)	-0.01	0.003
Arrival date : Year (1980)	0.81	0.28
Arrival date : Year (1981)	0.36	0.19
Arrival date : Year (1982)	0.26	0.41
Arrival date : Year (1983)	0.26	0.38
Arrival date : Year (1984)	0.12	0.14
Arrival date : Year (1985)	0.001	0.25
Arrival date : Year (1986)	-0.48	0.46
Arrival date : Year (1987)	-0.03	0.18
Arrival date : Year (1988)	0.003	0.17
Arrival date : Year (1989)	-0.38	0.20
Arrival date : Year (1990)	-0.27	0.57
Arrival date : Year (1991)	-0.21	0.39
Arrival date : Year (1992)	0.59	0.45
Arrival date : Year (1993)	0.33	0.45
Arrival date : Year (1994)	0.53	0.45
Arrival date : Year (1995)	NA	NA
Arrival date : Year (1996)	0.68	0.47
Arrival date : Year (1997)	-0.14	0.25
Arrival date : Year (1998)	0.02	0.40
Arrival date : Year (1999)	-0.52	0.59
Arrival date : Year (2000)	-0.26	0.69

Table S4.8. (cont.)

Number of fledglings	Estimates	s.e.
Arrival date : Year (2001)	0.43	2.59
Arrival date : Year (2002)	-0.31	1.08
Arrival date : Year (2003)	10.36	2.38
Arrival date : Year (2004)	-0.46	1.22
Arrival date : Year (2005)	0.10	0.22
Arrival date : Year (2006)	-1.26	0.42
Arrival date : Year (2007)	0.20	0.46
Arrival date : Year (2008)	-2.43	1.00
Arrival date : Year (2009)	0.18	0.15
Arrival date : Year (2010)	-0.04	0.25
Arrival date : Year (2011)	0.16	0.13
Arrival date : Year (2012)	-0.11	0.21
Arrival date : Year (2013)	0.26	0.13
Arrival date : Year (2014)	0.32	0.17
Year (1980)	-9.22	4.98
Year (1981)	-0.58	3.84
Year (1982)	1.04	7.24
Year (1983)	1.52	5.75
Year (1984)	4.04	2.79
Year (1985)	7.73	4.84
Year (1986)	13.85	7.78
Year (1987)	7.62	3.05
Year (1988)	6.62	2.55
Year (1989)	13.22	4.00
Year (1990)	11.96	10.54
Year (1991)	9.85	8.97
Year (1992)	-3.53	7.91
Year (1993)	2.55	6.85
Year (1994)	-0.17	7.60
Year (1995)	2.57	2.21
Year (1996)	-5.64	7.59
Year (1997)	9.66	4.87
Year (1998)	7.11	6.23
Year (1999)	15.23	9.15
Year (2000)	9.45	9.13
Year (2001)	-0.98	40.06
Year (2002)	10.47	14.76
Year (2003)	-106.30	25.61
Year (2004)	15.38	17.32
Year (2005)	6.47	2.93
Year (2006)	23.93	6.12
Year (2007)	3.26	6.27
Year (2008)	42.95	14.15
Year (2009)	3.11	2.73
Year (2010)	7.86	4.53
Year (2011)	4.12	1.88
Year (2012)	8.33	3.10
Year (2013)	1.54	1.93
Year (2014)	0.93	2.60

Table S4.9. Estimates and standard errors for the multiple regression analyses testing the effects of arrival date of the female and year on the probability of obtaining recruits.

Probability of obtaining recruits	Estimates	s.e.
Arrival Date^2 : Year (1980)	-0.02	0.02
Arrival Date^2 : Year (1982)	0.005	0.01
Arrival Date^2 : Year (1983)	-0.03	0.03
Arrival Date^2 : Year (1984)	-0.004	0.005
Arrival Date^2 : Year (1985)	-0.001	0.01
Arrival Date^2 : Year (1986)	-0.01	0.01
Arrival Date^2 : Year (1987)	-0.0002	0.003
Arrival Date^2 : Year (1988)	0.001	0.005
Arrival Date^2 : Year (1989)	-0.0005	0.01
Arrival Date^2 : Year (1991)	-0.003	0.01
Arrival Date^2 : Year (1992)	-0.07	0.08
Arrival Date^2 : Year (1993)	0.00	0.02
Arrival Date^2 : Year (1994)	-0.04	0.05
Arrival Date^2 : Year (1996)	0.004	0.01
Arrival Date^2 : Year (1997)	-0.05	0.04
Arrival Date^2 : Year (1998)	-0.01	0.02
Arrival Date^2 : Year (1999)	0.03	0.02
Arrival Date^2 : Year (2000)	-0.13	0.16
Arrival Date^2 : Year (2001)	-0.05	0.18
Arrival Date^2 : Year (2002)	-0.09	0.08
Arrival Date^2 : Year (2003)	0.01	0.01
Arrival Date^2 : Year (2004)	-0.28	0.28
Arrival Date^2 : Year (2005)	-0.04	0.04
Arrival Date^2 : Year (2006)	0.03	0.02
Arrival Date^2 : Year (2007)	-0.03	0.03
Arrival Date^2 : Year (2008)	0.01	0.04
Arrival Date^2 : Year (2009)	-0.03	0.02
Arrival Date^2 : Year (2010)	0.003	0.01
Arrival Date^2 : Year (2011)	-0.0002	0.01
Arrival Date^2 : Year (2012)	-0.03	0.03
Arrival Date : Year (1980)	1.24	1.22
Arrival Date : Year (1982)	-0.39	0.61
Arrival Date : Year (1983)	1.59	1.62
Arrival Date : Year (1984)	0.26	0.37
Arrival Date : Year (1985)	-0.01	0.59
Arrival Date : Year (1986)	0.45	0.81
Arrival Date : Year (1987)	0.03	0.22
Arrival Date : Year (1988)	-0.05	0.28
Arrival Date : Year (1989)	0.003	0.40
Arrival Date : Year (1991)	0.13	1.24
Arrival Date : Year (1992)	4.05	4.64
Arrival Date : Year (1993)	-0.42	1.37
Arrival Date : Year (1994)	2.36	2.72
Arrival Date : Year (1996)	-0.27	0.63
Arrival Date : Year (1997)	2.95	2.31
Arrival Date : Year (1998)	0.81	0.96
Arrival Date : Year (1999)	-1.87	0.99
Arrival Date : Year (2000)	6.34	7.77
Arrival Date : Year (2001)	2.41	10.58
Arrival Date : Year (2002)	4.91	4.53
Arrival Date : Year (2003)	-0.69	0.73
Arrival Date : Year (2004)	14.48	14.53
Arrival Date : Year (2005)	2.37	2.27
Arrival Date : Year (2006)	-1.75	0.91
Arrival Date : Year (2007)	1.52	1.59

Table S4.9. (cont.)

Probability of obtaining recruits	Estimates	s.e.
Arrival Date : Year (2008)	-1.10	2.42
Arrival Date : Year (2009)	1.32	1.15
Arrival Date : Year (2010)	-0.38	0.57
Arrival Date : Year (2011)	-0.14	0.34
Arrival Date : Year (2012)	1.75	1.76
Year (1980)	-22.25	22.09
Year (1982)	7.29	10.79
Year (1983)	-24.41	23.98
Year (1984)	-5.78	6.75
Year (1985)	1.67	10.71
Year (1986)	-7.07	13.28
Year (1987)	-1.72	3.70
Year (1988)	-0.75	4.26
Year (1989)	-1.08	7.60
Year (1991)	0.27	25.53
Year (1992)	-59.24	68.70
Year (1993)	6.35	18.78
Year (1994)	-32.06	38.95
Year (1996)	3.66	10.22
Year (1997)	-40.83	33.02
Year (1998)	-13.03	14.34
Year (1999)	29.69	15.37
Year (2000)	-75.47	92.36
Year (2001)	-29.83	155.30
Year (2002)	-70.81	64.26
Year (2003)	8.11	8.86
Year (2004)	-184.40	189.90
Year (2005)	-36.19	33.37
Year (2006)	22.82	12.45
Year (2007)	-20.96	19.66
Year (2008)	17.06	32.30
Year (2009)	-16.27	14.94
Year (2010)	7.40	8.75
Year (2011)	2.39	3.76
Year (2012)	-24.19	23.31